Behaviour and spatial ecology of Gilbert's dragon *Lophognathus gilberti* (Agamidae: Reptilia)

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Abstract

We examined the behavioural and spatial ecology of *Lophognathus gilberti*, a medium-sized, diurnal, dragon lizard that is commonly found in urban areas of north-western Australia. Males defend daily activity areas against other males, but not females. Both males and females shift their daily activity area on sequential days. *Lophognathus gilberti* use sight and perhaps auditory cues to locate prey, which consists mostly of invertebrates. They catch a prey item every 92 minutes, or 6-7 items each day, most often by sprinting from an elevated perch, but they do not actively search in leaf litter for prey. Three different stationary postures were observed; defensive, vigilant and aggressive. Males also have a courting posture that involves head bobbing, body pressing and tail twitching. These lizards often wave a forelimb and bob their heads after each short sprint. Movement is most often bipedal, with males moving greater distances (37.8 m h^{-1}) than females (13 m h^{-1}). When active, *L. gilberti* are most often found in full shade, and within 5 m of vegetation cover. They are constantly vigilant and are capable swimmers, diving to the bottom to avoid capture.

Keywords: Gilbert's dragon, *Lophognathus gilberti*, behaviour, ecology

Introduction

Lophognathus gilberti, Gilbert's dragon or "Ta Ta" lizard, is abundant in north-western Australia. The name "Ta Ta" lizard also applies to other species in this genus. This medium-size dragon lizard is readily observed because of its conspicuous colouration, active behaviour, and abundance in urban environments. One of the most distinctive features of this lizard, from which it derives its common name, is the rapid waving (circumduction) of its forefeet after each short sprint. Given its abundance there is surprisingly little information about this agamid lizard. James & Shine (1985) indicate they are reproductively active from September to February. Christian *et al.* (1999) report that the ecologically and morphologically similar *Lophognathus temporalis* are more active around Darwin (wet-dry tropics) during the wet season than the dry season, resulting in them being more visible and having significantly higher energy expenditure and water fluxes during the wet season.

Blamires (1998) reported that *L. temporalis* use circumduction as a distraction display to potential predators. Head bobbing and circumduction are most often performed by juvenile *L. temporalis*, and mainly when they were on the ground; these movements are independent of the presence of conspecifics. Large adult male *L. temporalis* employ head bobbing exclusively during the breeding season; this movement generally follows fleeing from a potential predator. Our observations of *L. gilberti* before this study suggested that males may defend territories, head-bobbing and forelimb waving may be a means of communicating with conspecifics, and that colour changes might be part of male's threat display and/or used to regulate body temperature.

Lophognathus gilberti is particularly abundant along the edges of permanent waterways (lakes, rivers, irrigation channels) around Kununurra. During September and October of 1999 we systematically observed these lizards in their natural environment with the specific objectives of examining a) their movement and activity patterns, b) interactions between males, between females, and between males and females, and c) association between body colour and behaviour.

Methods

The study site was a cleared rectangular area 18 m x 50 m along the northern edge of Lake Kununurra (UTM 0470068, 8253996). There was a steep bank of about a metre to the water. The water's edge contained a number of trees, a narrow band of thick vegetation, reeds and open areas. Three large trees, 3-5 m in from the water's edge, provided large areas of shade for most of the day in a cleared area beyond the vegetation at the lake's edge. People and vehicles moved through the area on a regular basis so that *L. gilberti* were habituated to their presence. Nevertheless, these lizards were constantly vigilant and would rapidly move to avoid being threatened.

Lophognathus gilberti emerged, basked and were active in the study area before 0730 each day. Observations prior to the study indicated that *L. gilberti* very seldom ventured toward the northern boundary of the study area

during the middle of the day because it was mostly in the sun and there was little vegetation cover. *Lophognathus gilberti* were observed for a total period of approximately 19 hours; one hour each day between 0955 and 1630 hours for most days between 26 September and 16 October, 1999. Observations were made by either of the authors who sat in a shady elevated position beyond the northern boundary of the study area. Seven of the observations commenced before noon; the remainder were in the afternoon. The location of lizards in the study area could be observed from this position, except when they climbed the far side of a tree, moved into thick vegetation along the banks of Lake Kununurra, or moved over the edge of the bank down toward the water.

At the beginning of each observational period, every *L. gilberti* present within the area was allocated a number and its sex was gauged by its shape and colour; adult males are generally darker grey or black, and have a larger head. There were no juveniles or sub-adults present in the area during the study period. Ambient air temperature was recorded in the shade approximately one metre above the ground at the commencement of each observation period, using a digital thermometer. The location, posture, movement, colour, behaviour and feeding of every *L. gilberti* present in the study area were recorded for each 5 minute period during a one hour observation.

A detailed map of the study site was prepared and overlayed with a 1 x 1 m grid so the exact location of each lizard and its movements could be accurately recorded. Every time a lizard moved, its new location was recorded. To determine the distance that a lizard moved, we presumed each lizard started and finished in the centre of a 1 x 1 m grid. We calculated the minimum distance that a lizard moved as the distance between the centre of the two grids *i.e.* where the lizard began and where it finished. We only included data where we had continuous visual contact with the lizard for a minimum of 25 min. If the lizard was disturbed by the presence of people or a vehicle, then all of its data were excluded. Total distance moved during a period of continuous observation (greater than 25 min) was divided by observation time in minutes, and is reported as distance moved in m h^{-1}. Body colour was described as dark, medium or light, and the location of the lizard in the sun, partial shade or complete shade was recorded every 5 minutes. Every time that a lizard caught a prey item was recorded; if prey could be identified then this was also recorded.

We made notes on all observations that might assist us to explain *L. gilberti's* behaviour and use of space. Incidental notes of the behaviour of specimens outside the study area were also used to supplement behavioural descriptions of lizards monitored in the study area.

Results

The mean ambient temperature at the commencement of each observation period was 34.2 (± se 0.65) °C. The sky was overcast for only one entire observation period (6 October), and no lizards were observed between 1530 and 1630 hours in the study area on this occasion. Surface soil temperature in the sun was measured at the commencement of an observation session on eight occasions. For those occasions, mean surface soil temperature in the sun was 53.3 (± se 3.19) °C, and ambient air temperature in the shade, one metre above the ground, was 35.0 (± se 1.07) °C. Other than on 6 October, there was always some portion of the study site that was exposed to direct sunlight.

There was no difference (*t* test, $P = 0.71$) in the number of males and females observed within our study site boundaries during an hour observation period. The mean number of females observed was 2.4 (± se 0.30, range 0–5 at any one time) and the mean number of males observed was 2.6 (± se 0.32, range 0–5 at any one time).

Body colour

Female *L. gilberti* never attain the very dark/black body colour apparent for males. In shade, 53% of the observations of male lizards were dark grey/black, 19% were medium brown and 28% were light brown (Fig 1). For females in shade, 39% were light brown and 61% were dark brown. The dense tree canopy meant there were few areas with partial shade; as a consequence there was little opportunity for lizards to be found in these conditions. *Lophognathus gilberti* preferred to stay out of direct sunlight, with only 11% of observations for males and 8% of observations for females occurring in direct sunlight. When in direct sunlight, 42% of males were light coloured and 39% were medium coloured. The remaining 19% were dark brown or black. For females in direct sunlight, 81% had a medium brown body colour, and 19% were light brown.

Feeding

During 3040 lizard minutes of observation, *L. gilberti* were seen to catch 33 prey items; this is equivalent of one item of prey every 92 min. It was not always possible to discern what was caught, as many of the items were small and swallowed quickly. We only observed invertebrates being caught. The general feeding strategy was to remain motionless on an elevated perch (*e.g.* tree stump, elevated surface tree root, low branch, pile of vegetation) watching for potential prey. Prey were generally detected visually but we saw lizards looking in the direction of noises in the leaf litter suggesting that they might also use auditory cues. Having detected potential prey the lizard would sprint to the location from its observation post. These sprints were rarely longer than 2 m, but we did observe sprints of up to 5 m to catch prey. Two males were seen to jump unsuccessfully in an attempt to catch flying insects. An adult male *L. gilberti* which captured a large grasshopper took 20 min to subdue and devour it; another male took 40 min to subdue and devour a dragonfly. Much of the time taken to eat these large prey items appeared to be associated with aligning prey in their mouth so that it was eaten head first. Most of the invertebrates captured were in leaf litter or close to leaf litter.

Posture

Only a small range of stationary postures were adopted;

- defensive – arched (convex) back and tail along the ground, inflated abdomen;
- vigilant – head up with arched (concave) back, tail down and head tilted or moved in accordance with what the animal was observing;

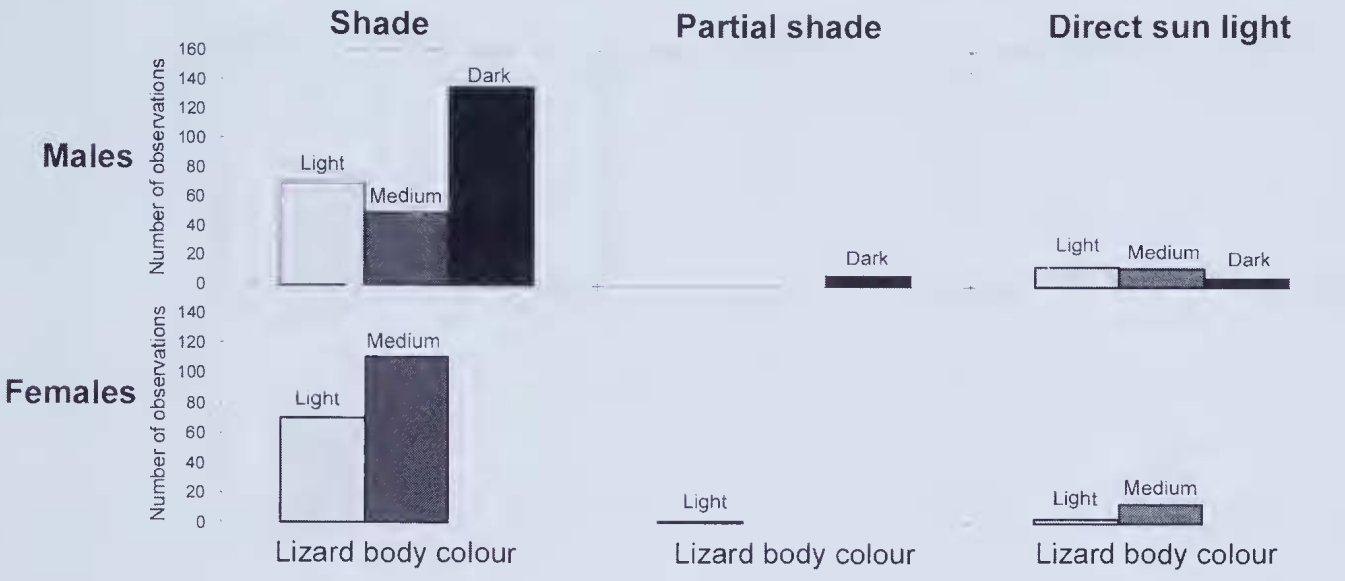

Figure 1. Body colour of male and female *L. gilberti* in shade, partial light and direct sun light.

- aggressive (males only) – arched (concave) back, forelimbs almost straight elevating the chest, head erect at about 45° to the horizontal;
- males courting – head bobs, body presses, body colour was mostly black and the tail often twitches.

We observed a number of *L. gilberti* with their tail arched over their back so that the tip was almost above the head. A female almost always waved her forelimb after sprinting a short distance, unless it was attempting to catch prey. Males also waved their forelimbs, but less often, and this action was often accompanied with a few quick head bobs. There was a slow and a fast head bob. The slow movement was most often accompanied by an arching at the neck. *Lophognathus gilberti* would sometimes head bob while stationary in the vigilant posture.

Movement patterns

Males moved a significantly greater distance per hour than females (*t*-test, two sample unequal variance, $P < 0.01$; we appreciate there is some replication of individuals in this comparison, but it was not possible to individually identify all lizards from day to day). We observed undisturbed females continuously for in excess of 25 min on 15 occasions and during that time they moved at a rate of 13.3 (± se 3.61, range 0–42.4) m h^{-1}. We observed undisturbed males continuously for in excess of 25 min on 27 occasions and during that time they moved at a rate of 37.8 (± se 5.67, range 1-127.3) m h^{-1}. Although it was not quantified, females appeared more timid, retreating to cover earlier than males when threatened.

Lophognathus gilberti rarely walked, and most movements were short sprints to catch a prey item, to chase another lizard, to avoid an attack by another lizard, or to avoid a person, vehicle or potential predator (*Varanus mertensi* and *V. mitchelli*). Most of the time *L. gilberti* sprinted bipedally, although they seemed unable to run bipedally on loose leaf litter. *Lophognathus gilberti* would rapidly climb a tree when threatened. On two occasions we saw a *V. mertensi* move through the study area and on one occasion we saw a *V. mitchelli* move through the area. On these three occasions, all *L. gilberti* observed these potential predators before we did and rapidly moved to the cover of dense vegetation. We observed *L. gilberti* on numerous occasions more than 2.5 m up a tree, mostly in their vigilant posture. To avoid detection they would often move around to the other side of the tree when approached. They were observed to jump from low branches or tree trunks over 0.5 m to the ground and jump over 0.3 m from the ground to tree trunks. These dragon lizards were rapid and agile movers along thick branches of trees. They appeared to avoid narrow branches, which they would only use if there was no other option and they were being pursued by a potential predator.

We never observed *L. gilberti* retreating to a burrow in the ground. We occasionally found them sleeping on trunks of large trees at night. We observed females occasionally digging shallow holes, often out in the open, which we presumed were 'test holes' for egg laying. We found no evidence that movement behaviour altered with the time of day (*e.g.* morning *vs* afternoon).

Use of space

On only 9.7% of occasions were *L. gilberti* observed more than five metres from a tree or other vegetation. Twenty six of 33 prey items were caught within 5 m of vegetation cover. On every occasion where we witnessed a confrontation between two lizards, the aggressor displaced the lizard being attacked suggesting that there was an established hierarchy, and that each lizard responded according to its place in that hierarchy. Large males with black colouration would generally not tolerate another similar-coloured male within its activity area; the activity area appeared to be defined as the space in which it was foraging at that time. In a male-male encounter, the aggressor would sprint straight at the other male. Most often the male being attacked would see the approaching male and would rapidly leave the area. We observed only one fight between males, and this was outside the study area. In this instance, a large male

chased and caught another male. A brief battle followed; movements were very quick and specific actions were difficult to observe. It appeared that the attacker rapidly bit the other male on the neck, back and legs. The attacked male fled after a couple of seconds. We observed a second encounter between two similar-sized males that lasted for approximately 5 - 6 minutes. Both males had obviously seen each other from a distance of at least 10 m. They slowly approached to within 0.6 m of each other. Both lizards were in direct sun light (ambient temperature in the shade was 33 °C and surface soil temperature was 42.5 °C) and their colour was light brown, throat and chests were enlarged, and their crests were erect. One had its tail in the air and the other flicked its tail from side-to-side. Both lizards slowly raised and lowered their heads as they moved in a circle but maintained their distance apart (about 0.6 m). Eventually both males retreated to shade some 15 m apart, never getting closer than about 0.5 m. On one occasion we observed a large male lizard attack a bar-shouldered dove (*Geopelia humeralis*) on the ground; after a few bites the dove flew off. On other occasions *G. humeralis* were regularly seen on the ground within metres of *L. gilberti*.

Males regularly chased female *L. gilberti*. On most occasions the female quickly fled to the cover of vegetation. If the female moved into an open area the male often followed, and the female again moved away from the male. We observed a female *L. gilberti* to lie flat on the ground on three occasions when a male moved near, presumably to avoid detection. On only one occasion did we observe a male catch and mount a female. There was no obvious copulation as the female displaced the male and moved off within a couple of seconds. We observed one male *L. gilberti* chase a female into an open area, where the female remained in the sun for several minutes, eventually opening its mouth presumably to lose heat by evaporation.

We endeavoured to track individual lizards on sequential days but without clear markings to identify each lizard we could not be certain that we correctly identified all animals each day. However, we were able to positively identify a few of the *L. gilberti* based on their body size and obvious external markings (*e.g.* cut tail). These recognisable individuals moved their activity area on sequential days. From this we concluded that the daily activity area for most lizards changed from day-to-day. However, most of the recognisable lizards remained in the general area as we frequently saw a particular lizard using the same or adjacent area every couple of days.

When disturbed or fleeing from a predator, *L. gilberti* would, as a last choice, dive into the water. They swam rapidly to the bottom, and would swim through bottom vegetation until they stopped and remained motionless. On two occasions we watched specific sites where a *L. gilberti* were last seen in the vegetation on the bottom of a shallow clear waterway for in excess of 30 min and did not see these lizards move, nor were we able to find these lizards in a subsequent search.

Discussion

The rate of movement of males and females around their activity areas differed. Males moved more often and covered greater distances probably because they chased other males, females and prey items. Females, in contrast, only flee from males and chase prey items. *Lophognathus gilberti* is an accomplished arboreal lizard that uses tree trunks and low branches as observational perches. They appear reluctant to move around on narrow branches, possibly because their relatively long hindlimbs impede rapid movement along narrow branches. This conclusion concurs with those of Losos & Sinervo (1989) who report sprint speed of long-limbed *Anolis* on thin rods being slower than for species with shorter limbs.

Body colour appeared to be influenced by whether *L. gilberti* were in sun or shade. For males, their body colour was generally darker in shade than in sun, and lighter in sun than in shade. A lighter body colour would minimise solar heat absorbance, and lightening of body colour is a strategy used by other lizards to minimise the potential for heat stress in direct sunlight (Pianka *et al.* 1998). In contrast, more females were dark brown than light brown in sun and shade. The number of individuals that had a dark body colour in sun when ambient air and surface soil temperatures where high enough to lift the lizard's body temperature close to their thermal maximum (presumed to be 42–45 °C, see Curry-Lindahl 1979), suggests that body colour might also be used for camouflage or communicating with other conspecifics. Attacking males were usually dark grey or black in colour, but this was not always the case. Therefore we could not conclude that the dark colour of male *L. gilberti* was part of a threat display.

Lophognathus gilberti spent most of their active time close to vegetation cover. This could be for one of a number of reasons. Surface soil temperature in sun during periods when these dragon lizards were active was generally in the low 50s °C. Remaining in the sun on soil at this temperature even for relatively short periods would result in heat stress (Curry-Lindahl 1979). The dark body colour would presumably further reduce the maximum period of time these lizards could remain in the sun because of higher radiative absorbance. Secondly, most of the potential prey might be near vegetation. Seventy nine percent of prey were caught within 5 m of vegetation, which may either reflect where prey were, where lizards were or movement into open areas increased the risk of predation.

Within the study site, aggression by one male towards another invariably led to the attacked male leaving the area. There are at least two plausible explanations for this behaviour. Firstly, a strong hierarchy had been established among males, and subordinate males were generally not prepared to contest their rank in the hierarchy, or alternatively males are defending 'todays' territory. The only extended encounter observed between two similar-sized males did not result in physical contact, suggesting both adversaries were endeavouring to assert their dominance without fighting. This may have been because the body temperature of both males was near their critical thermal maximum. Males showed no aggression (*e.g.* charging, biting) toward females as might have been expected, given that males would normally want to attract females. Females regularly moved from their perch when males moved toward them. We observed no evidence of female–female aggression, although we observed smaller females moving away from larger females when they approached. These data

suggest that females do not aggressively defend daily activity areas, but there may be a recognised hierarchy based on body size.

Activity area of male *L. gilberti* shifted on a daily basis. Daily activity areas of males at any given time did not overlap and a male often defended space that was occupied by other males on other days. Our data therefore indicate that home ranges (combined activity areas over many days) for male *L. gilberti* overlapped and daily activity areas shifted with little site fidelity from one day to the next. Shifting daily activity areas could reflect the search for prey or the search for receptive females (Pough *et al.* 1998).

Body colour, head and chest bobbing, and circumduction are all signs of lizard communication (Ferguson 1977; Gibbons 1979). What was not obvious from our observations was the purpose of some of these communications. Females waved their forelimb almost every time they moved (unless they captured prey) and this action occurred immediately upon ceasing to run. Males more often bobbed their heads at the conclusion of a short sprint, but they also waved their forelimbs. Blamires (1998) suggests that circumduction by *L. temporalis* is used to distract potential predators or to indicate to potential predators that their presence has been noted to discourage further pursuit. He also reported that juveniles waved their forelimbs more often than adults, and this is mainly done on the ground. There were no juveniles present in our study area and we observed circumduction independent of the apparent presence of predators and conspecifics. Therefore we do not agree with Blamires' (1998) interpretation of the purpose for this movement, although we are unable to suggest an alternative.

When a female was present males often rapidly bobbed their heads, did some quick 'body presses' and twitched the end of their tail. In this circumstance we presumed that this was part of the male courtship display. Males that can see each other were observed to arch their necks and slowly bob their heads. This often preceded an attack. We concluded that the arched neck and slow head bobbing was part of the display of dominance and defence of the activity area. Blamires (1998) reported the purpose of head bobbing was a threat display by large males, and was only used during the breeding season. Although James & Shine (1985) reported *L. gilberti* to be sexually active from September to February, we only saw one male mount a female and given the female displaced the male within a couple of seconds it is unlikely they copulated. All other advances by males were rejected by females, suggesting it was not the breeding season. Our view is that fast head-bobbing by males is used for courtship display and the slow head-bobbing with an arched neck and back is a threat display.

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